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Response of bark beetles and their natural enemies to fire and fire surrogate treatments in mixed-conifer forests in western Montana

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ABSTRACT

Four treatments (control, burn-only, thin-only, and thin-and-burn) were evaluated for their effects on bark beetle-caused mortality in both the short-term (one to four years) and the long-term (seven years) in mixed-conifer forests in western Montana, USA. In addition to assessing bark beetle responses to these treatments, we also measured natural enemy landing rates and resin flow of ponderosa pine (*Pinus ponderosa*) the season fire treatments were implemented. All bark beetles were present at low population levels (non-outbreak) for the duration of the study. Post-treatment mortality of trees due to bark beetles was lowest in the thin-only and control units and highest in the units receiving burns. Three tree-killing bark beetle species responded positively to fire treatments: Douglas-fir beetle (*Dendroctonus pseudotsugae*), pine engraver (*Ips pini*), and western pine beetle (*Dendroctonus brevicomis*). Red turpentine beetle (*Dendroctonus valens*) responded positively to fire treatments, but never caused mortality. Three fire damage variables tested (height of crown scorch, percent circumference of the tree bole scorched, or degree of ground char) were significant factors in predicting beetle attack on trees. Douglas-fir beetle and pine engraver responded rapidly to increased availability of resources (fire-damaged trees); however, successful attacks dropped rapidly once these resources were depleted. Movement to green trees by pine engraver was not observed in plots receiving fire treatments, or in thinned plots where slash supported substantial reproduction by this beetle. The fourth tree-killing beetle present at the site, the mountain pine beetle, did not exhibit responses to any treatment. Natural enemies generally arrived at trees the same time as host bark beetles. However, the landing rates of only one, *Medetera* spp., was affected by treatment. This predator responded positively to thinning treatments. This insect was present in very high numbers indicating a regulatory effect on beetles, at least in the short-term, in thinned stands. Resin flow decreased from June to August. However, resin flow was significantly higher in trees in August than in June in fire treatments. Increased flow in burned trees later in the season did not affect beetle attack success. Overall, responses by beetles to treatments were short-term and limited to fire-damaged trees. Expansions into green trees did not occur. This lack of spread was likely due to a combination of high tree vigor in residual stands and low background populations of bark beetles.

1. Introduction

Many western North American fire-dependent forests possess considerably different compositions and structures than they did historically. These changes have been brought about primarily by fire suppression, high-grade harvesting, and livestock grazing (Gruell et al., 1982; Arno and Brown, 1989; Arno et al., 1995; Hessburg and Agee, 2003). In many cases, forests are now denser, contain more small and fewer large diameter trees, have greater fuel continuity, higher fuel loads, and increased ladder fuels (Agee, 1993; Arno et al., 1997). These conditions can adversely affect forest ecosystem integrity, function, and resilience, and increase the probability of unnaturally severe wildfires (Stephens, 1998).

As recognition of the negative effects of fire suppression and some harvesting practices has grown, so has the drive to implement treatments to reduce the threat of severe wildfire and restore affected stands to more natural and functional conditions. Treatments recommended to achieve these goals most often involve thinning, prescribed fire, or a combination of the two. While these approaches are already in widespread practice, their efficacy in meeting objectives, and their impacts on forest ecosystems are mostly unknown. To address this lack of knowledge, the Joint Fire Science Program funded the National Fire and Fire Surrogate (FFS) Study (http://www.fs.fed.us/ffs/), a five-year

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project to investigate the effects of alternative fire and fire surrogate treatments, not only in reducing fire hazard, but also on sustainability of forest resources and ecological function. Eleven sites participated across the United States, each implementing similar, replicated, statistically rigorous, operational-scale experiments that included assessments of fire and fire surrogate treatments on forest structure and composition, fuels, understory vegetation, soils, wildlife, insects, tree diseases, and economics.

Four treatments (control, burn-only, thin-only, and thin-and-burn) were evaluated in the FFS Study. These were chosen because they represent the primary treatment options available, and those most commonly used by managers for hazard reduction and forest restoration. In addition, they address the four major hypotheses underlying many forest restoration projects in fire-adapted North American forests (Weatherspoon, 2000). These hypotheses and their relationship to treatments in this study are (1) forest ecosystems are best restored/conserved with no direct manipulation of ecological processes (fire) or structure (thinning) except for a continuation of fire suppression (control treatment), (2) forest ecosystems are best restored/conserved by restoring ecosystem processes (reintroducing or allowing fire to occur) (burn-only treatment), (3) forest ecosystems are best restored/conserved by restoring ecosystem structure (thin-only treatment), and (4) restoration and conservation of forest ecosystems requires both process and structural restoration (thin-and-burn treatment).

We focused on the impacts of alternative fire and fire surrogate treatments on tree mortality due to bark beetles at the FFS Lubrecht Experimental Forest site in western Montana. This site consists of ponderosa pine–Douglas-fir forests. This forest type is adapted to, and maintained by, low intensity and mixed-severity fires, but can be severely damaged by high-severity stand-replacement fires (Mutch et al., 1993; Brown et al., 1994; Arno et al., 1995). Historically, at this site, and across vast areas of the western United States, frequent low intensity fires removed competing shade-tolerant species and maintained large tree-dominated open stands with a diverse understory (Arno, 1980; Hessburg and Agee, 2003). However, since the turn of the century, ponderosa pine–Douglas-fir forests have been subjected to heavy harvesting, grazing, and intense fire suppression efforts. This has resulted in a predominance of overdense stands, composed mainly of younger trees, and a shift away from dominance by shade-intolerant ponderosa pine to shade-tolerant species, particularly Douglas-fir.

Our objective in this study was to determine how alternative fire and fire surrogate treatments influence mortality of trees due to bark beetles in ponderosa–Douglas-fir forests. Little work has focused on understanding the factors influencing bark beetle dynamics in this forest type in the Northern Rocky Mountains and most recommendations for beetle management are based on the works conducted in other, often quite different, forest systems such as lodgepole pine or southwestern ponderosa pine.

In conifer forests, in general, overdense stands are believed to be more susceptible to bark beetles than more openly spaced stands due to the reduced vigor, and consequently lower defensive capabilities, of individual trees resulting from inter-tree competition for water, nutrients and sunlight (Kolb et al., 1998; Skov et al., 2004; Wallin et al., 2004). The defensive systems of conifers consist of preformed and induced responses (Franceschi et al., 2005). Preformed defenses typically consist of constitutive resin that is released as beetles bore through bark to access the phloem where mating, egg laying and larval development occur (Franceschi et al., 2005; Raffa et al., 2005). This "primary" resin acts as a physical defense, smothering or repelling beetles when produced in sufficient quantities. While primary resin contains monoterpenes and other secondary defense chemicals, these chemicals are not typically present in concentrations high enough to negatively affect beetles or their symbiotic fungi (Franceschi et al., 2005; Raffa et al., 2005). Induced defenses, on the other hand, are not in place before the insects arrive, but rather form in response to insect or pathogen entry (Franceschi et al., 2005; Raffa et al., 2005). Induced responses typically involve the development of lesions around the invading beetle that becomes soaked with "secondary" resin which contains toxic levels of monoterpenes, but which can also smother beetles and their eggs. Both defensive systems are energetically expensive and typically only vigorous trees with substantial energy reserves produce these to their fullest capacity (Franceschi et al., 2005). Weakened or stressed trees, on the other hand, typically reserve energy stores for vital functions and present little in the way of defense (Franceschi et al., 2005).

While reducing tree density, through either thinning or the use of prescribed fire, can sometimes ultimately result in increased vigor of residual trees and greater resistance to bark beetles (Larsson et al., 1983; Waring and Pitman, 1985; Brown et al., 1987; Wallin et al., 2008), it is important to realize that the effects of such treatments can vary greatly depending upon a number of factors including beetle species, tree species, the scale of time since treatment (short- and long-term effects) and beetle population size. This is true, not only because many bark beetle species differ substantially in their life histories and responses to environmental conditions, but also because conifer species vary considerably in the type and strength of defensive system (Lewinsohn et al., 1991a,b) and the degree and rapidity of response they exhibit to density reduction treatments or to fire damage (Ryan and Reinhardt, 1988).

In mixed-conifer forests in western Montana, the main tree-killing bark beetles are the mountain pine beetle (*Dendroctonus ponderosae* Hopkins), the western pine beetle (*Dendroctonus brevicomis* LeConte), and the pine engraver (*Ips pini* (Say)) in pines, and the Douglas-fir beetle (*Dendroctonus pseudotsugae* Hopkins) in Douglas-fir (Furniss and Carolin, 1977). Another common bark beetle, the red turpentine beetle (*Dendroctonus valens* LeConte), typically colonizes living pines without causing mortality except under unusual conditions where populations reach exceptionally high levels (Smith, 1971; Ganz et al., 2003; Fettig et al., 2006). Each of these beetle species has a distinctive life history and different ecological requirements, and thus, may respond differently to each of the four treatments in the FFS Study. Our objective was to monitor beetle-caused mortality in stands before and after treatment, in both the short- and long-term, and determine which treatments most influence increases or decreases in beetle activity. In addition, because arthropod natural enemies (parasitoid wasps, and predatory flies and beetles) are considered regulators of bark beetle populations in the non-outbreak phase (conditions at Lubrecht Forest during the study), we assessed the effects fire and fire surrogate treatments have on natural enemy abundance in the short-term. In conjunction with the natural enemy study, we also measured resin flow in ponderosa pines, to assess short-term effects of treatments on preformed defenses against bark beetles.

The FFS was funded for a period of five years (2000–2004) that allowed collection of one year's pretreatment data and four years' post-treatment data. This effort resulted in robust information on short-term responses of bark beetles to the four treatments in the ponderosa pine–Douglas-fir forest type. However, to fully understand whether treatments achieve management objectives, and how they affect bark beetle populations over the long-term, periodic resurveys of study plots will be required. Our first long-term assessment of the FFS Study plots at Lubrecht Forest was conducted in summer 2008, eight years post-initiation of the study. The results of the first five years of the project as well as the eighth year survey are presented in this article.

2. Methods

2.1. Study site

The study site is located at the University of Montana's Lubrecht Experimental Forest near Greenough, Montana (47° north latitude, 113° west longitude). Forests at Lubrecht consist primarily of ponderosa pine and Douglas-fir with lesser components of western larch and lodgepole pine. All the trees used in the study were second growth stands regenerated after heavy harvesting in the early 1900s when almost all large diameter trees were removed. The site has also been subjected to moderate grazing over the last hundred years, and although low intensity high frequency fires occurred in these forests in the past (Arno, 1980; Brown et al., 1994), these stands have not experienced burning since the late 1800s. Conditions at Lubrecht Forest are representative of vast areas across the western United States.

2.2. Experimental design and treatments

The study was deployed in a randomized block design. Three 36-ha blocks were established in ponderosa pine–Douglas-fir forests on gentle to moderate slopes. Each block was divided into four units of 9 ha each. One replicate of each treatment was assigned to one unit in each block. All units were of similar forest type and elevation and treatments were assigned randomly. A 6×6 grid of reference points with equal 50 m spacing between points was placed in each unit. This resulted in 36 points per unit, 144 points per block, and 432 points total for the experiment.

Treatments were designed to move stands toward a desired range of conditions that mimicked pre-fire suppression, pre-logging forests in the region. This target was defined as stands comprising $\geq$90% seral species (ponderosa pine, western larch, and lodgepole pine) with $<$10% shade-tolerant Douglas-fir. Stands exhibiting target conditions would be relatively open and dominated by larger trees with a random clumpy spatial distribution (Metlen and Fiedler, 2006). In accordance with the FFS Study, target conditions included that each non-control treatment achieve stand and fuel conditions, that if the area was impacted by a head fire under 80th percentile weather conditions, at least 80% of the basal area of the overstory would be expected to survive (Weatherspoon, 2000).

2.2.1. Thin-only

Thinning treatments were designed to re-establish ponderosa pine as the dominant stand component, and to establish conditions that would favor its continued regeneration. The target basal area for thinning treatments was 11 m^2/ha. Thinning was conducted in winter when soils were frozen. Logs were removed but all non-merchantable material was left in place and trampled by harvest machinery.

2.2.2. Burn-only

Prescribed fires were conducted in late spring using a strip fire technique under relative humidities of 20–48%. Flame lengths varied from 0.2 to 1.2 m. The fire treatment reduced pre-burn duff depths of 2.0–0.6 cm. Fires burned relatively patchy in these stands, with some areas burning fairly hot resulting in considerable mortality of small diameter trees, while other areas remained relatively untouched.

2.2.3. Thin-and-burn

Thinning in these units was conducted as described under Section 2.2.1. Prescribed fires were conducted at the same time and under the same conditions as described for the burn-only treatment. Flame lengths varied from 0.2 to 2.7 m. The fire treatment reduced pre-burn duff depths of 2.0–0.5 cm. Fire burned somewhat patchy, but more uniformly than in the burn-only treatments.

2.2.4. Control

Control stands were not thinned or burned.

2.3. Timing of treatments and post-treatment surveys

Blocks, units and point grids were established in spring 2000. Thinning was conducted in winter 2001. Prescribed fires were conducted in late spring (May and June) 2002. Pretreatment surveys were conducted in 2000. Post-thinning surveys began in summer 2001 and post-fire surveys began in summer 2002 (a month after burning was completed). Thus by the end of the five-year project, we had, in addition to pretreatment data, four years post-thinning data and three years post-burn data. Our follow-up survey in summer 2008 provided long-term data for effects of treatments seven years post-thinning and six years post-burning.

2.4. Bark beetle assessments

A circular 0.04-ha plot (one-tenth of an acre) was established in summer 2000 at each grid point in each unit of each block. The following characteristics were recorded for each tree $>$10 cm DBH (diameter breast height) in each plot: tree species, DBH, and height. From plot center, the azimuth, bearing, and distance to each tree were recorded so that the fate of individual trees could be followed for the duration of the study. For tree-killing bark beetles (mountain pine beetle, western pine beetle, Douglas-fir beetle, and pine engraver), attacks on trees in plots each year were rated as successful (attacks with brood production and tree killed) or unsuccessful (attacks without brood production and tree not killed). For the red turpentine beetle, which does not typically kill trees, its presence or absence on each tree was recorded. For all bark beetles, the year of attack was recorded. The year of attack of trees killed by beetles was determined using a combination of previous years survey results, foliage color (green, yellow, red, and silver), and amount of needles retained on tree.

2.5. Fire assessments

In summer 2002, immediately after fire treatments were implemented, all trees $>$10 cm DBH in plots in units receiving fire treatments were assessed for degree of fire severity experienced during the burns. We used three measures to assess severity: crown scorch height (distance from ground to highest point of crown exhibiting scorch), percent circumference of bark scorched at the soil line, and degree of ground char using a method modified from Ryan and Noste (1985). Ground char was rated on a scale of 0–5. A zero rating was assigned when no charring of the soil around the base of the tree was observed. A rating of 1 was assigned when light ground char was observed. Light ground char was defined as $<$1% of the area deeply charred, $<$15% moderately charred, and the remaining area lightly charred or unburned. A rating of 2 was assigned when light/moderate ground charring occurred. In this case, between 1 and 10% of the area around the base of the tree was deeply charred, but $<$15% was moderately charred. A rating of 3 was assigned for moderate ground char. In this case, $\leq$10% of the area was deeply charred and $>$15% was moderately charred. A rating of 5 was assigned for heavy ground char where $>$10% of the area was deeply charred and $>$80% moderately charred. A more detailed description of the ground char classification can be found in Ryan and Noste (1985).

2.6. Natural enemy assessments

In mid-June 2002, we established random transects across treatment units in one randomly chosen block (Block 1) of the FFS study. At a spacing of 20 m along the transect we located 10 ponderosa pines (20 cm DBH or greater) (40 trees total). Around the bole of these trees at 1.4 m above the ground we attached 0.5 m × 0.9 m sections of metal hardware cloth screening (0.3 cm mesh) sprayed with Tangle Trap (The Tanglefoot Co., Grand Rapids, MI). Screens were collected and replaced weekly starting June 19 and ending August 2. All insects stuck to the screens were removed and transferred to vials containing 90% ethanol. The insects were then sorted and identified as bark beetles (to genus), Cleridae (predatory beetles), parasitoid wasps, or *Medetera* spp. (predatory flies), and their abundance recorded.

2.7. Resin flow

In July 2002, one month after burns were complete, and again in August of the same year, we established random transects in each treatment unit in all three blocks. Along each transect we selected 8 ponderosa pines (96 trees total) (25 cm DBH or greater) at an approximate spacing of 20 m to measure resin flow. A 2.5 cm arch punch was used to remove a circular piece of bark and phloem from the north and south sides of each tree (first sampling period) or the west and east sides of each tree (second sampling period). A small aluminum funnel was attached below the hole where the bark had been removed and inserted into a plastic graduated 15 ml centrifuge tube to capture resin released from the punch site. Tubes were left in place for 24 h to capture resin. After 24 h, the tubes were removed and the amounts of resin in each tube recorded.

2.8. Data analysis

Repeated measures ANOVA was used to detect differences among years (time), treatments, and time × treatment for each bark beetle species. While data were not normally distributed and could not be normalized using transformations, the large sample size in our study allows the use of this more robust test. Mean separations were conducted using Bonferroni's multiple range test.

To test for the effects of fire damage to trees on likelihood of attack by bark beetles, logistic regression models were run using crown scorch height, percent circumference of bole scorched, and ground char rating as independent variables. Also included, as independent variables, were tree DBH and height. These tests were conducted by beetle species for ponderosa pine (mountain pine beetle, pine engraver, western pine beetle, and red turpentine beetle), lodgepole pine (mountain pine beetle, pine engraver, and red turpentine beetle) and Douglas-fir (Douglas-fir beetle). Data for the burn-only and thin-and-burn treatments, and for bark beetle activity for three post-treatment years (2002–2004), were combined for use in the regressions.

Captures of bark beetles and natural enemies on sticky screens were analyzed using one-way ANOVA with block, treatment or sample time as independent variable. Differences in resin flow within sampling periods were analyzed using one-way ANOVA with block, treatment, or sample time as independent variables. Differences in resin flow by sampling time and treatment were analyzed using paired *t*-tests. Mean separations were conducted using Bonferroni's multiple range test.

All analyses were conducted using Statistix 7 (Analytical Software, 2000).

3. Results

3.1. Stand characteristics

Stands were relatively dense prior to the initiation of the study (Table 1). Thin-only and thin-and-burn treatments substantially reduced stand density and basal area and target densities and basal areas were met (Table 1). Burn-only treatments reduced density, but did not achieve target density and basal area goals (Table 1).

3.2. Treatment effects: 2000–2004

Summary statistics for bark beetle activity by tree species and treatment for the five-year study are presented in Table 2.

No Douglas-fir beetle-killed trees were found in any units during the pretreatment survey in 2000, or in 2001 after the completion of thinning treatments (Fig. 1). This continued to be the case in the control and thin-only units for all five years. In units receiving prescribed burn treatments (burn-only and thin-and-burn), several trees were killed by Douglas-fir beetle soon after burns were conducted (2002), as well as in the year following burning (2003) (Fig. 1). However, by the second year after burning, and continuing through to 2004, no additional mortality due to

Table 1
Starting and ending basal areas (m^2/ha) and stand densities by block and treatment for the Fire and Fire Surrogate Study at Lubrecht Experimental Forest, MT.

Block	Treatment	Basal area 2000	Basal area 2005	Trees/ha 2000	Trees/ha 2005
1	Thin-only	19.33	10.71	325	122
2	Thin-only	20.78	13.60	448	180
3	Thin-only	21.66	12.01	397	170
1	Thin-and-burn	16.12	10.57	297	139
2	Thin-and-burn	23.32	9.74	425	122
3	Thin-and-burn	23.61	9.36	346	91
1	Burn-only	24.09	24.01	509	475
2	Burn-only	25.70	21.59	475	337
3	Burn-only	18.62	19.29	342	347
1	Control	16.11	17.14	344	353
2	Control	24.30	25.29	424	426
3	Control	31.39	32.34	425	421

Table 2
Number (%) of successfully attacked trees for mountain pine beetle (MPB), western pine beetle (WPB), pine engraver (PE), and Douglas-fir beetle (DFB), and presence of attacks for red turpentine beetle (RTB) by tree species and treatment in experimental plots at Lubrecht Forest, MT (2000–2004).

Treatment	Douglas-fir		Ponderosa pine					Lodgepole pine			
	N	DFB	*N*	MPB	WPB	PE	RTB	*N*	MPB	PE	RTB
Control	530	0 (0)	685	8 (1.16)	0 (0)	10 (1.5)	9 (1.31)	2	0 (0)	0 (0)	0 (0)
Thin-only	123	0 (0)	853	1 (0.12)	0 (0)	2 (0.02)	56 (6.57)	15	0 (0)	1 (6.67)	2 (13.3)
Thin-and-burn	75	15 (20.0)	298	1 (0.34)	2 (0.67)	31 (1.04)	125 (42.0)	12	0 (0)	6 (50.0)	5 (41.7)
Burn-only	507	30 (6.0)	915	25 (2.73)	8 (0.87)	34 (0.37)	121 (13.2)	37	11 (33.3)	11 (33.3)	22 (59.5)
Totals	1235	45 (3.64)	2751	35 (1.27)	10 (0.36)	77 (2.80)	224 (8.14)	66	11 (16.7)	18 (27.3)	29 (43.9)

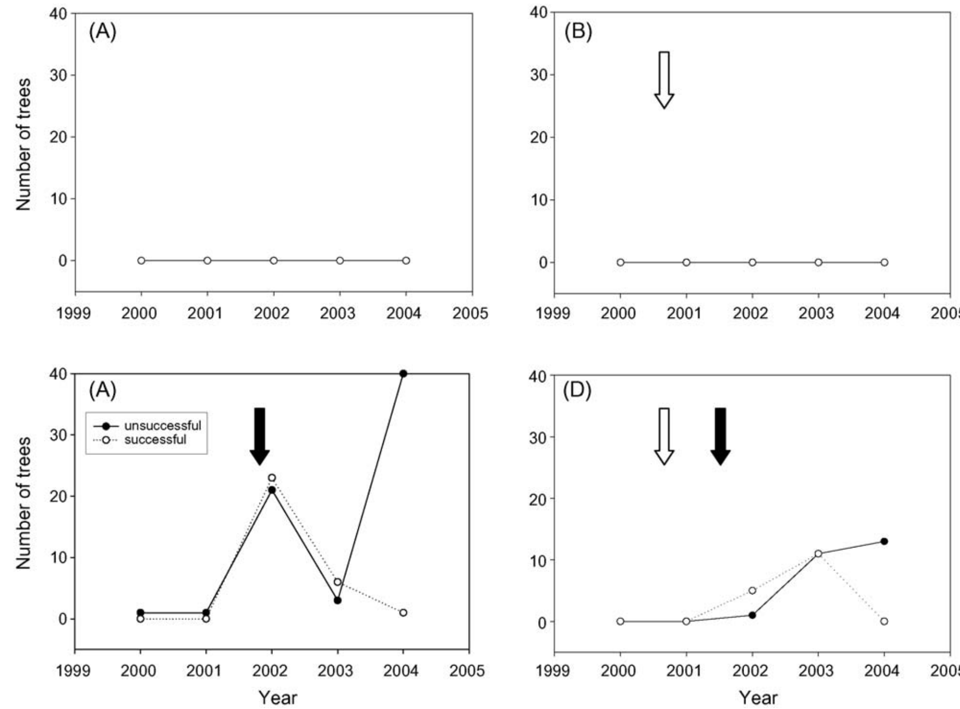

Fig. 1. Number of Douglas-fir killed by Douglas-fir beetle in (A) control, (B) thin-only, (C) burn-only and (D) thin-and-burn treatments at Lubrecht Forest, MT (2000–2004). Open arrows indicate timing of thinning treatments; bold arrows indicate timing of burn treatments.

Douglas-fir beetle was observed in either of these treatments (Fig. 1). The effects of time (year), treatment, and the interaction between time and treatment were all highly significant for this insect ($F = 8.62$, df = 4, $P < 0.0001$; $F = 8.55$, df = 3, $P < 0.0001$; $F = 6.02$, df = 12, $P < 0.0001$, respectively).

Small numbers of ponderosa pines were killed by pine engraver in 2001 and 2002 in the control units, and in 2002 in the thin-only treatments (Fig. 2). However, relatively high numbers of ponderosa pines were killed in the thin-and-burn treatment units immediately after burning (2002) and in the year after fire (2003), and in the burn-only treatment units in the year after fire (2003) (Fig. 2). In both of these treatments, pine engraver populations returned to low, baseline levels by the second year after fire (2004) (Fig. 2). The effects of time and treatment were significant for this beetle

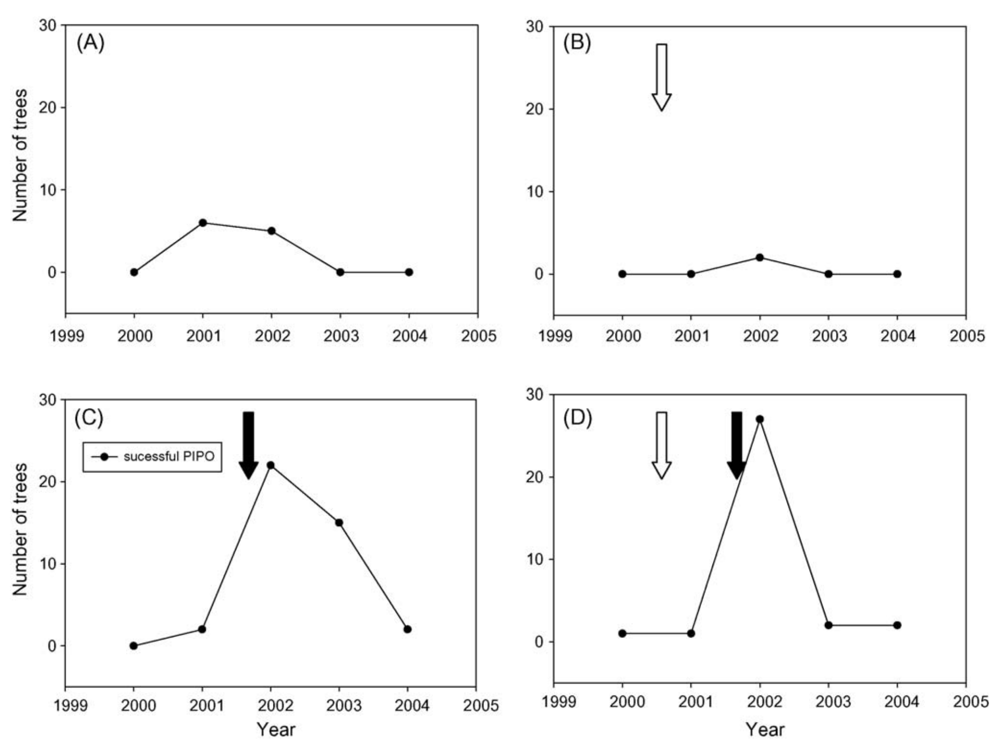

Fig. 2. Number of ponderosa pines (PIPO) killed by pine engraver in (A) control, (B) thin-only, (C) burn-only and (D) thin-and-burn treatments at Lubrecht Forest, MT (2000–2004). Open arrows indicate timing of thinning treatments; bold arrows indicate timing of burn treatments.

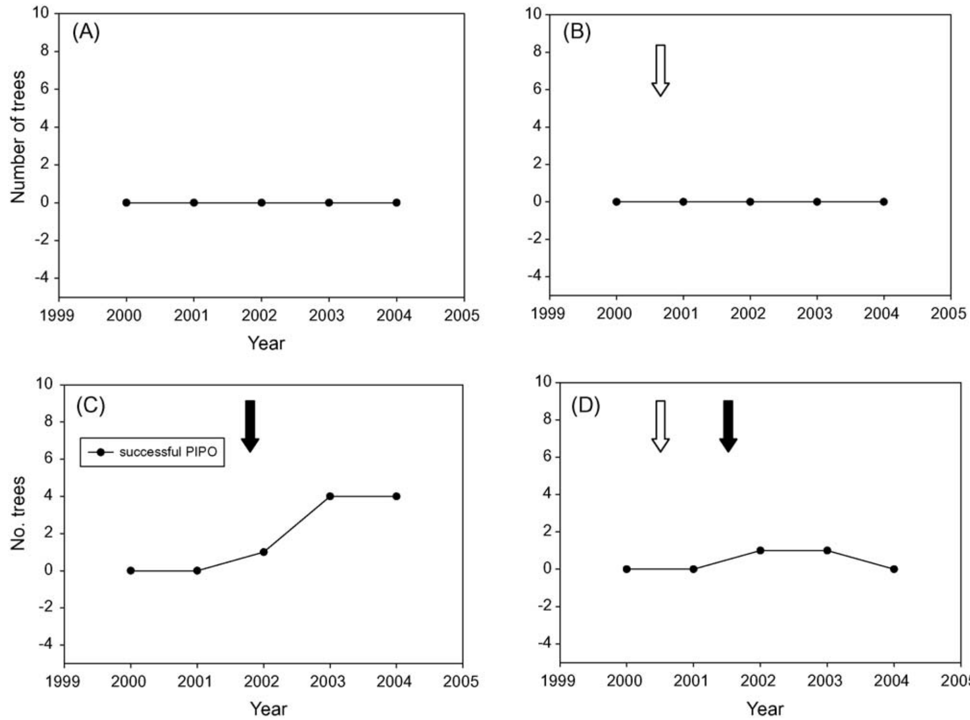

Fig. 3. Number of ponderosa pines (PIPO) killed by western pine beetle in (A) control, (B) thin-only, (C) burn-only and (D) thin-and-burn treatments at Lubrecht Forest, MT (2000–2004). Open arrows indicate timing of thinning treatments; bold arrows indicate timing of burn treatments.

($F = 5.15$, df = 4, $P = 0.0004$; $F = 8.42$, df = 3, $P < 0.0001$, respectively), but not the interaction between time and treatment ($F = 1.47$, df = 12, $P = 0.1277$).

Like the Douglas-fir beetle, the western pine beetle was not detected in any experimental units in the first two years of the study, but it killed trees in the burn-only and thin-and-burn treatments soon after burns were implemented (Fig. 3). In the thin-and-burn treatment, a very small number of ponderosa pines were killed in both 2002 and 2003, but none in 2004 (Fig. 3). In the burn-only treatment, a small number of ponderosa pines were killed in 2002, 2003 and 2004 (Fig. 3). For this beetle, the effects of time and treatment were significant ($F = 6.91$, df = 4, $P < 0.0001$; $F = 6.01$, df = 3, $P = 0.0005$, respectively), but not the interaction between time and treatment ($F = 1.61$, df = 12, $P = 0.0813$).

A small number of ponderosa pines were killed by mountain pine beetles in all blocks in 2000. A small increase in numbers of ponderosa pines killed by this beetle was observed in 2001 in all units except in those slated for burn-only treatments where numbers of ponderosa pines killed increased greatly (Fig. 4). By 2002, numbers of ponderosa pines killed by mountain pine beetle declined in all treatments, and by 2003, numbers of ponderosa pines killed across all treatments were very low. There was a moderate increase in the mortality of ponderosa pines in 2004 in control, thin-only, and thin-and-burn treatments (Fig. 4). In the burn-only treatment, mortality of ponderosa pine due to mountain pine beetle decreased in the year after fire (2003) while mortality of lodgepole pine due to the beetle, which had been non-existent until that point, increased greatly (Fig. 4). By 2004, mortality of ponderosa pine in the burn-only treatment was again increasing, while mortality of lodgepole pine dropped back to zero (Fig. 4). For this beetle, the effects of time, treatment, and the interaction between time and treatment were significant ($F = 4.60$, df = 4, $P = 0.0011$; $F = 9.90$, df = 3, $P < 0.0001$; $F = 1.83$, df = 12, $P < 0.0387$, respectively).

Red turpentine beetle was present in the control units in low numbers and remained low in number in this treatment throughout the study (Fig. 5). In the thin-only units, the number of trees colonized by the beetle fluctuated from year to year but remained low overall. In the burn-only treatment, beetles increased greatly in 2001 (the year before burning), remained high the year burns were conducted, and then plummeted to nearly zero the year after the fire (Fig. 5). In the thin-and-burn treatment, there was a small increase in trees colonized by this beetle in 2001, a large increase in 2002, and then a drop to near zero in 2003 (Fig. 5). In both the burn-only and the thin-and-burn treatments, there was a small increase in number of trees attacked in 2004 (Fig. 5). The vast majority of trees attacked by this beetle were ponderosa pines, although lodgepole pines were also attacked in substantial numbers in the burn-only treatment units after burning treatments were implemented (Table 2). For this beetle, the effects of time, treatment, and the interaction between time and treatment were significant ($F = 19.55$, df = 4, $P = 0.0001$; $F = 20.49$, df = 3, $P < 0.0001$; $F = 6.07$, df = 12, $P < 0.0001$, respectively).

For mountain pine beetle and Douglas-fir beetle, we tracked unsuccessful as well as successful attacks over time. For the Douglas-fir beetle, in the thin-and-burn and burn-only treatments, the number of successfully and unsuccessfully attacked trees was nearly equal until 2004 when the number of successfully attacked trees dropped to near zero, while the number of unsuccessfully attacked trees subsequently increased.

For the mountain pine beetle, only unsuccessful attacks were observed on pines in the control units (Fig. 5). In the thin-only units, the same was true except that one ponderosa pine was successfully attacked in 2003. For trees in the thin-and-burn units, most attacks were unsuccessful except for one ponderosa pine killed in 2003 and one in 2004. The number of unsuccessful attacks in this treatment increased greatly in 2004 but with no subsequent increase in successful attacks. In the burn-only treatment units, there were a number of successful attacks by mountain pine beetle on ponderosa pine but most of these occurred the year prior to burning (2001). The number of ponderosa pines killed by the beetle

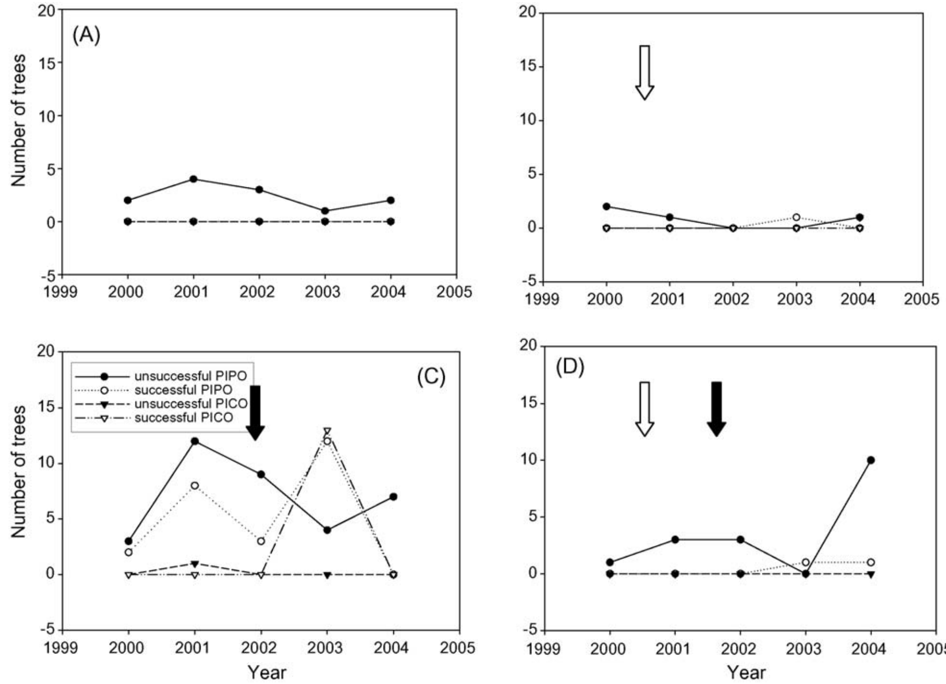

Fig. 4. Number of ponderosa pine (PIPO) or lodgepole pine (PICO) killed by mountain pine beetle in (A) control, (B) thin-only, (C) burn-only and (D) thin-and-burn treatments at Lubrecht Forest, MT (2000–2004). Open arrows indicate timing of thinning treatments; bold arrows indicate timing of burn treatments.

declined gradually after 2001, reaching a low point in 2003 (the year after burning) and then rose again slightly in 2004. Unsuccessful attacks in ponderosa pine in the burn-only treatment followed the same general trend as successful attacks in 2000, 2001, and 2002, but exhibited opposite trends to successfully attacked trees in 2003 and 2004, rising as successful attacks dropped. Patterns of successful and unsuccessful attacks in lodgepole pine were different from those in ponderosa pine. Beetle activity in lodgepole pine was essentially not detected in any plots in 2000–2002 except for one unsuccessfully attacked tree. All subsequent activity occurred in burn-only units. In 2003, there was a strong spike in successful attacks in lodgepole pine, followed by a drop to zero successful attacks in 2004. Unlike in ponderosa pine and Douglas-fir, the drop in the number of successful attacks was not accompanied by a subsequent rise in unsuccessful attacks in this tree species.

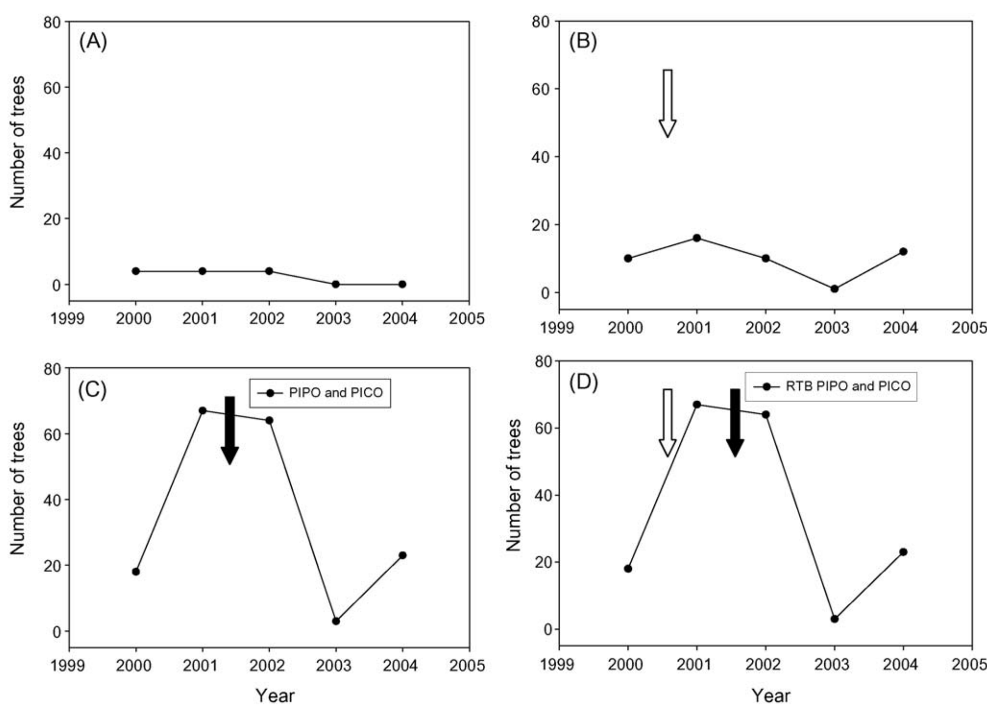

Fig. 5. Number of ponderosa pine (PIPO) or lodgepole pine (PICO) colonized by red turpentine beetle in (A) control, (B) thin-only, (C) burn-only and (D) thin-and-burn treatments at Lubrecht Forest, MT (2000–2004). Open arrows indicate timing of thinning treatments; bold arrows indicate timing of burn treatments.

Table 3
Mean (sd) crown scorch height, ground char rating, percent circumference of tree bole charred, DBH, and height of trees in experimental plots receiving prescribed burning treatments at Lubrecht Forest, MT (measured in 2002 after completion of prescribed burns).

Treatment	Douglas-fir		Ponderosa pine		Lodgepole pine	
	N	Mean (sd)	*N*	Mean (sd)	*N*	Mean (sd)
Thin-and-burn	79		113		12	
Crown scorch height (m)		11.59 (6.58)		13.73 (6.68)		17.68 (3.34)
Ground char[a]		3.77 (1.24)		3.13 (1.06)		3.42 (1.31)
% Bole charred		87.9 (61.3)		82.73 (26.28)		84.17 (28.03)
DBH (cm)		31.78 (8.58)		32.3 (12.1)		24.56 (6.58)
Tree height (m)		19.11 (3.80)		19.61 (4.64)		18.25 (3.28)
Burn-only	445		916		36	
Flame length (m)		7.98 (5.89)		8.33 (7.34)		8.73 (5.90)
Ground char		2.61 (1.00)		2.38 (0.81)		2.08 (0.50)
% Bole charred		67.80 (37.16)		61.52 (32.79)		61.11 (36.72)
DBH (cm)		25.85 (8.25)		27.28 (9.95)		20.28 (4.63)
Tree height (m)		15.95 (3.34)		17.47 (3.98)		15.28 (2.42)

[a] Uncharred = 1, low char = 2, moderate/low char = 3, moderate char = 4, and high char = 5 (modified from Ryan and Noste, 1985).

3.3. Treatment effects: 2005–2008

Mortality of trees due to bark beetles remained very low from the end of the five-year FFS Study through summer 2008 when we resurveyed plots. No additional mortality of trees due to Douglas-fir beetle, western pine beetle, or pine engraver was observed in any of the plots. Mountain pine beetle killed an additional 11 trees in the three-year period between surveys. Six of these occurred in control plots, four in burn-only plots and one in thin-and-burn plots. Not only were red turpentine beetle attacks found mostly in thin-and-burn plots (13 trees), but also in thin-only plots (4 trees), and burn-only plots (4 trees). No red turpentine beetle attacks were observed in control plots.

3.4. Fire damage effects

Summary statistics for the independent variables (crown scorch height, percent circumference of bole charred, degree of ground char, tree DBH, and tree height) used in logistic regression analyses are presented in Table 3.

3.4.1. Ponderosa pine

One thousand and twenty-nine ponderosa pines from burned plots were included in regression analysis. None of the independent variables tested exhibited significant effects on likelihood of successful attack by the mountain pine beetle (Table 4). This was also true for western pine beetle (Table 4). However, the number of trees killed by the western pine beetle was extremely low, so these results should be considered with caution. In contrast, the likelihood of successful attack by pine engraver was significantly affected by percent circumference charred, ground char, crown scorch height, and DBH (Table 4). Mean crown scorch height was higher (16.4 m, sd = 4.4 m) for trees killed by pine engraver than for trees not killed by pine engravers (9.5 m, sd = 7.3 m). For trees killed by pine engraver, mean ground char rating (3.40, sd = 1.09) and percent circumference scorched (96.48, sd = 8.41) were also higher than for trees not killed by pine engraver (2.48, sd = 0.89; 66.19, sd = 33.07, respectively). Mean DBH of trees killed by pine engraver in burn-only and thin-and-burn treatments was 24.58 cm (sd = 8.25 cm) compared with 28.43 cm (sd = 10.23 cm) for trees that were not killed by pine engraver.

The likelihood of attack by red turpentine beetle was also significantly affected by crown scorch height, percent circumference charred, degree of ground char, and DBH (Table 4). Mean crown scorch height, percent circumference charred, ground char rating and DBH in attacked trees (14.3 m, sd = 5.9 m; 88.65, sd = 21.03; 3.09, sd = 1.03; 30.25 cm, sd = 10.4 cm, respectively) were all higher than in un-attacked trees (8.9 m, sd = 7.3 m; 64.91, sd = 33.23; 2.44, sd = 0.88; 28.23 cm, sd = 10.20 cm, respectively).

3.4.2. Douglas-fir

Five hundred and twenty-four Douglas-fir were included in logistic regression analyses. Crown scorch height, percent circumference of bole charred, ground char and DBH had significant effects on likelihood of successful attack by this beetle (Table 4). Mean crown scorch height, percent circumference charred, ground char rating, and DBH in attacked trees (14.4 m, sd = 4.5 m; 95.47, sd = 12.40; 3.42, sd = 1.12; 30.25 cm, sd = 7.45 cm, respectively) were all higher than in un-attacked trees (7.6 m, sd = 5.9 m; 68.72, sd = 42.50; 2.70, sd = 1.08; 26.25 cm, sd = 8.55 cm, respectively).

3.4.3. Lodgepole pine

Lodgepole pine was a very minor component of stands in this study; only 48 lodgepole pine trees were present in burn-only and thin-and-burn plots. None of the independent variables tested exhibited significant effects on likelihood of successful attack by the mountain pine beetle, pine engraver or red turpentine beetle except DBH for pine engraver (Table 4).

3.5. Natural enemy and bark beetle landing rates

The total number of *Dendroctonus* spp. and natural enemies captured on sticky screens is presented by treatment in Table 5. Most bark beetles (*Dendroctonus* and *Ips*) were captured on sticky screens early in the trapping period, and most prior to 3 July. The effect of time on the number of *Dendroctonus* captured was highly significant ($P < 0.0001$, df = 8, 378, $F = 21.80$) with more beetles arriving in the first trapping period than in subsequent trapping periods. However, the effect of treatment was not significant ($P = 0.202$, df = 3, 383, $F = 1.55$). *Ips* were captured only in the first two trapping periods. The number of *Ips* captured was too low to analyze for time or treatment effects.

Natural enemies varied in the timing of their arrival at traps. Clerids arrived at traps over the entire trapping period, but the biggest peak in numbers coincided with the peak arrival of bark beetles. A smaller peak occurred later in the season but only in the thin-only treatment. The effect of time on arrival at traps was significant ($P < 0.00001$, $F = 7.22_{9,376}$) with the greatest numbers arriving in the first three trapping periods. There was no effect of treatment ($P = 0.4782$, $F = 0.83_{3,383}$). By far, the most abundant natural enemy captured on sticky traps was *Medetera* spp., which exhibited an early peak coincidence with the arrival of host beetles; however, while bark beetle captures dropped to low or zero levels after 3 July, these flies continued arriving at trees

Table 4
Coefficients and statistics for logistic regression models of bark beetle attacks on trees in plots treated with prescribed fire.

Independent variable	Coefficient	Standard error	Wald's statistic	*P*-value
Douglas-fir				
Douglas-fir beetle				
Char	0.000478	0.000456	1.101	<0.001
Ground char	0.345	0.162	4.517	0.034
Flame length	0.0667	0.0136	23.964	<0.001
DBH	0.148	0.0654	5.137	0.023
Tree height	−0.0376	0.0225	2.801	0.094
Ponderosa pine				
Mountain pine beetle				
Char	0.0149	0.0108	1.901	0.168
Ground char	0.124	0.292	0.179	0.672
Flame length	0.00605	0.00627	0.930	0.335
DBH	−0.110	0.110	1.00	0.317
Tree height	−0.00925	0.0295	0.0982	0.754
Western pine beetle				
Char	0.0190	0.0190	1.003	0.317
Ground char	0.156	0.422	0.136	0.712
Flame length	0.0102	0.00675	2.277	0.131
DBH	−0.215	0.156	1.898	0.168
Tree height	0.0543	0.0423	1.651	0.199
Pine engraver				
Char	0.0757	0.0188	16.197	<0.001
Ground char	0.673	0.162	17.203	<0.001
Flame length	0.0144	0.00502	8.237	0.004
DBH	−0.124	0.0607	4.199	0.040
Tree height	−0.0180	0.0169	1.130	0.288
Red turpentine beetle				
Char	0.0244	0.00534	20.923	<0.001
Ground char	0.338	0.107	9.987	0.002
Flame length	0.0171	0.00528	10.524	0.001
DBH	−0.0575	0.0362	2.530	0.112
Tree height	0.0221	0.0118	3.521	0.061
Lodgepole pine				
Mountain pine beetle				
Char	−0.0427	0.0345	1.532	0.216
Ground char	0.000000144	0.00000086	0.0282	0.867
Flame length	0.0111	0.0624	0.0315	0.859
DBH	0.300	0.708	0.180	0.671
Tree height	0.00273	0.212	0.000165	0.990
Pine engraver				
Char	−0.0317	0.0221	2.049	0.152
Ground char	0.000000131	0.000000561	0.0548	0.815
Flame length	0.0998	0.0756	1.743	0.187
DBH	1.043	0.446	5.463	0.019
Tree height	−0.249	0.140	3.171	0.075
Red turpentine beetle				
Char	−0.0591	0.0378	2.452	0.117
Ground char	−0.000000516	0.000000607	0.723	0.395
Flame length	0.215	0.177	1.476	0.224
DBH	−0.568	0.447	1.617	0.203
Tree height	−0.104	0.198	0.274	0.601

throughout the trapping period. The number of *Medetera* captured was highest in the thin-only and thin-and-burn treatments, and lowest in the control. The effect of time on the number of *Medetera* captured was highly significant ($P < 0.0001$, $F = 21.55_{8,378}$) with more flies arriving in the first two trapping periods than in subsequent trapping periods. The effect of treatment was also significant ($P = 0.0001$, $F = 9.45_{3,383}$), with traps in thinning treatments capturing the highest number of flies. Parasitoids (all Hymenoptera) were characteristically low in number. The effect of time on the number of parasitoids captured was significant ($P < 0.0001$, $F = 6.27_{8,378}$) with more parasitoids arriving in the first trapping period than in subsequent trapping periods. However, the effect of treatment was not significant ($P = 0.089$, $F = 2.19_{3,383}$).

Table 5
Total number of *Dendroctonus* spp., Cleridae, parasitoid Hymenoptera, and *Medetera* spp. (Dolichopodidae), captured on sticky traps in thin-only, burn-only, thin-and-burn, and control units, at Lubrecht Experimental Forest, MT in 2002.

Taxon	Thin-only	Burn-only	Thin/burn	Control	Total
Dendroctonus spp.	43	87	124	66	320
Cleridae	53	46	32	46	177
Hymenoptera	106	72	76	55	309
Medetera spp.	1930	1180	2029	701	5840

Table 6
Mean (sd) resin flow (ml) in ponderosa pines at Lubrecht Experimental Forest, MT, in 2002, by treatment and sampling period (burn treatments were implemented in June 2002, thinning treatments were implemented in winter 2001). Bold values indicate significant differences between sampling periods. Different letters after values indicate significant differences between treatments within the same sampling period.

Treatment	*N*	July	August
Control	24	**8.63** (**3.85**)[a]	**6.65** (**3.87**)[ab]
Thin-only	24	**9.32** (**4.60**)[a]	**5.72** (**3.81**)[b]
Thin-and-burn	24	9.80 (4.50)[a]	9.33 (5.61)[a]
Burn-only	23	**10.75** (**4.44**)[a]	**7.93** (**4.55**)[ab]

3.6. Resin flow

Mean (sd) resin flow by treatment and sampling date are presented in Table 6. Resin flow measurements taken in July did not differ by block ($P = 0.177$, $F = 1.76_{2,92}$) or treatment ($P = 0.246$, $F = 1.41_{3,91}$). Resin flow in August also did not differ by block ($P = 0.138$, $F = 2.03_{2,92}$) but differed significantly by treatment ($P = 0.040$, $F = 2.88_{3,92}$). Resin flow was highest in the thin-and-burn treatment, intermediate in the burn-only treatment and the control, and lowest in the thin-only treatment (Table 6). Resin flows were higher in July than in August in all treatments (Table 6) (control: $P = 0.032$, df = 23, $T = 2.29$; thin-only: $P = 0.006$, df = 22, $T = -3.07$; burn-only: $P = 0.005$, df = 23, $T = -3.10$) except the thin-and-burn treatment ($P = 0.6947$, df = 23, $T = -0.04$) where resin flow was relatively high in both periods.

4. Discussion

All bark beetles were present at low population levels (non-outbreak) for the duration of the study. However, despite low numbers, significant responses to treatments were detected for all species of interest. Post-treatment mortality of trees due to bark beetles was lowest in the thin-only and control units and highest in the units receiving burns. Three tree-killing bark beetle species responded positively to fire treatments: Douglas-fir beetle, pine engraver and western pine beetle. Douglas-fir beetle was undetectable in the study area until fire treatments were implemented. After burns, the beetle was found only in fire-treated areas. The increase in Douglas-fir beetle in these units, however, was short-lived, and occurred only in the year of treatment and one-year post-fire. While successful attacks on Douglas-fir increased immediately after fire, unsuccessful attacks increased greatly in the second year after fire, concomitant with a sharp drop in successful attacks. This strong shift from successful to unsuccessful attacks in the second year post-fire indicates that as suitable resources (fire-weakened trees) were depleted, the beetle was not able to move successfully into residual green trees. While few studies exist quantifying the temporal sequence of Douglas-fir beetle dynamics in fire-affected stands, especially beyond the first two years after burning, there does appear to be considerable variability in how long the beetle remains active, and whether the beetle moves into green trees once fire-damaged trees are depleted (Ryan et al., 1988; Amman and Ryan, 1991). This variability is likely due to the condition of trees in affected stands at the time of, and after, the fire, and the number of hosts available and suitable for supporting beetle population amplification (Peterson and Arbaugh, 1989). This beetle is mainly limited to attacking stressed or weakened trees, and cannot sustain outbreaks in vigorous stands. Therefore, the ability of this beetle to spread into green trees, and the length of time it can sustain successful attacks after fire, is likely directly linked to factors that increase the availability of susceptible trees, particularly drought. For example, the fires in Yellowstone National Park in 1988 affected large areas of forest containing Douglas-fir. Douglas-fir beetle responded to this increased availability of hosts by increasing the activity in affected stands for over four years post-fire including considerable spread into green trees (Amman and Ryan, 1991). This extended period of activity, and the ability of the beetle to move into green trees, was likely aided initially by high beetle numbers developing in widespread and abundant scorched trees, but then sustained by drought that affected the area at that time.

The preference of Douglas-fir beetle for fire-affected trees was significantly influenced by crown scorch height, percent circumference of bole charred, and degree of ground char, with trees with higher levels of damage in these categories significantly more likely to be killed by the beetle. Relationships between probability of attack by Douglas-fir beetle and these factors, especially crown scorch, have also been observed by others (Wyant et al., 1986; Ryan and Reinhardt, 1988; Peterson and Arbaugh, 1989; Amman and Ryan, 1991). In our study, we did not monitor severely damaged trees that were killed outright by fire. Such trees are typically not suitable for beetle development because of extreme damage to phloem resources. Considering only trees that survived fire, and thus were suitable hosts for the beetle, our data indicate that the beetle is most likely to cause mortality in trees that have been moderately damaged by fire. Our results also indicate that when residual trees in a stand are vigorous, and background populations of the beetle are low, the threat to trees that are most desirable for retention (unburned) is low, and that sanitation to prevent spread to green residual trees is likely unnecessary.

The pine engraver killed a few scattered trees prior to the initiation of fire treatments; however, the greatest increase in attacks by this beetle occurred in plots receiving fire treatments in the year after burning. These results were not surprising as this beetle is well known to respond strongly to fire-scorched trees (Amman and Ryan, 1991; Ganz et al., 2003). In this study, pine engravers responded rapidly to the increased availability of new resources, but like Douglas-fir beetle, successful attacks dropped rapidly once these resources were depleted. Movement to, and amplification in, green trees was not observed in plots receiving fire treatments, nor in thinned plots where abundant slash supported substantial reproduction by this beetle (D.L. Six, unpublished data). All three fire damage variables tested were significant factors predicting response by this insect. Pine engraver mortality was significantly influenced by DBH, with the beetle preferring the smaller diameter mature ponderosa pines in the stands. Like Douglas-fir beetle, the ability of this insect to move into green trees after build up in fire-affected trees is likely affected by relative vigor of the trees in stands at the time of, and immediately after, burning, and background levels of the insect.

The western pine beetle is also well documented to respond to fire-affected trees (Miller and Keen, 1960; McHugh et al., 2003; Perrakis and Agee, 2006). In this study, the number of trees killed by this beetle was very low, but we were still able to detect a significant effect of burn treatments. In contrast to the pine engraver, this beetle preferred larger diameter mature ponderosa pine.

The most abundant bark beetle in the study units was the red turpentine beetle (253 individual trees attacked over the course of the five-year study). While attacks by this beetle were commonplace, mortality of trees caused by this beetle was never observed, and attacks by this beetle did not predispose trees to subsequent attacks by other bark beetles. None of the trees attacked by the red turpentine beetle during the study died in subsequent years. Thus, while this beetle responded to fire treatments (and continued to do so after six years), its presence did not contribute to post-treatment mortality. Like the other beetle species that responded positively to fire-affected trees, red turpentine beetle also preferred trees with higher crown scorch height, greater percent circumference charred, and higher degree of ground char. It selected pines of larger diameter than those occurred on average in the stands.

Unlike the other bark beetle species monitored in this study, the mountain pine beetle did not exhibit a positive response to fire-affected trees. The mountain pine beetle, unlike the Douglas-fir beetle, pine engraver and western pine beetle, prefers, and is capable of maintaining outbreaks in stands of green, relatively vigorous trees. This very different ecological strategy is reflected in its selection behavior, with burned trees typically avoided for colonization (Ryan and Amman, 1994; Rasmussen et al., 1996; McHugh et al., 2003).

In this study, thinning had no detectable effect on beetle-caused tree mortality. This may, in part, be due to the low beetle population pressure at the site. The real test of thinning treatments, and the effects of fire on reducing stand density, and subsequently increasing tree vigor and resistance to beetle attack, will occur when study units are challenged by high beetle populations. A rapid expansion of mountain pine beetle, and to a lesser extent, pine engraver populations, is currently occurring at Lubrecht Forest and surrounds. Continued monitoring of the FFS Study units over the next several years will gain important information, not only on longer-term effects of treatments, but also on what occurs when treated stands are exposed to pressure from outbreak-level populations of beetles developing in adjacent unmanaged stands, a situation common in the western United States.

The arrival of natural enemies in treatment units coincided, for the most part, with the arrival of host beetles early in the summer. There was no effect of treatment on captures of bark beetles, clerid predators or parasitoid wasps. However, the most abundant natural enemy, the predacious fly, *Medetera*, was significantly more abundant in thinning treatments. This may have been due to a build up of this natural enemy in slash infested by pine engraver in thinned sites or to attraction of these flies to slash. *Medetera* have been shown to respond positively to host tree odors (e.g. cut short logs, Boone et al., 2008) and may have been attracted by monoterpenes and other secondary chemicals released from slash, stumps and damaged trees. If that is the case, the enhanced attraction of this predator is likely only transitory, and any potential increase in the regulation of bark beetle populations by increased predation is likely short-term. However, given that the build-up of bark beetles in slash and stumps produced by thinning operations can pose a threat to green trees under some circumstances, a short-term increase in these predators may play some regulatory role. Studies in Europe indicate that *Medetera* are important predators of the spruce beetle (reviewed in Wermelinger, 2004). Nagel and Fitzgerald (1975) found that individual larvae of *Medetera aldrichii* Wheeler (a common species in the western United States) consumed, on average, 7–15 Douglas-fir beetle larvae and that higher numbers of prey increased the mobility of the predator and its efficacy in locating and killing prey. Given its high abundance at our site and in association with bark beetles in other studies (Dahlsten and Stephen, 1974), further investigations of the impacts of this insect on bark beetle hosts may be warranted.

Resin flow in ponderosa pine decreased in all treatments from June to August. While resin flow did not differ by treatment in June, it did in August, with trees in burn treatments producing significantly more resin than trees in treatments without fire. Increased resin flow in fire-damaged trees has been previously documented and has been postulated to potentially increase resistance of trees to beetle attack (Feeney et al., 1998; Perrakis and Agee, 2006). In this study, most successful attacks on ponderosa pine by bark beetles occurred in June or early July so any effect on resin flow that occurred later in the season likely had no effect in deterring or preventing attacks. We did not measure resin flow the following year. However, if resin flow continued to be higher in fire-affected ponderosa pines, this effect did not translate to increased protection, as only fire-damaged trees were killed in years 1 and 2 after burning, consistent with the findings of Santoro et al. (2001) who found no decrease in insect activity after fire in eastern old-growth pine forests despite an increase in resin flow volume.

5. Conclusions

Overall, the mortality of trees due to bark beetles in the study blocks, as well as in the surrounding area, was low (non-outbreak phase) for the eight years covered in this study. Responses we observed for the five bark beetles species to the FFS treatments are likely to be representative of what would occur in similar mixed-conifer forests with low beetle populations. Given that these beetles typically exist in low densities, and that outbreaks are relatively rare over time, these are the conditions under which managers most often will need to implement treatments. Our results, therefore, should be useful in informing managers as to what types of responses they are likely to encounter and what beetle mitigation measures may need to be considered when implementing similar fire and thinning treatments. However, it is important to realize, that responses of these same beetle species to similar treatments may differ when beetle populations are high, or when long-term stress exists in forests at the time of treatment. Although many of the findings of this study have been similarly described from other studies, the value of these findings cannot be understated. Many past reports consist of anecdotal information, are based on opportunistic assessments of wildfires, or present the results of case studies. While such studies and observations are valuable, replicated, statistically rigorous, operational-scale experiments such as those conducted under the FFS Study, play an important role in providing strong empirical data to support decision-making regarding forest restoration and fuels management.

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